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Original article

Traces (ichnospecies *Oichnus paraboloides*) of predatory gastropods on bivalve shells from the Seogwipo Formation, Jejudo, Korea

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ABSTRACT

Circular to subcircular drill holes were identified on the bivalve shells collected from the Seogwipo Formation, Jejudo, Korea. A great majority of the drill holes (>70%) were found on the surfaces of a bivalve species *Glycymeris rotunda*. They are characterized by a beveled sharp edge and paraboloid in cross section with larger outer borehole diameter (OBD; mean 4.21 mm) and smaller inner borehole diameter (mean 2.94 mm). Walls of the drill holes are generally smooth, and walls ornamented with etched relief-like structures were also recognized. A slightly raised central boss observed in an incomplete specimen may indicate a failure of predator's attack. All drill holes collected are classified as a single ichnospecies *Oichnus paraboloides* Bromley, 1981. They are interpreted as boring traces produced by predatory gastropods, particularly naticid gastropods. Most *O. paraboloides* boreholes are observed in the central area of shell surfaces; a few boreholes lie marginally, which may reflect a borehole-site selectivity. No correlation between size of prey (shell height) and size of predator (OBD) is recognized. It is likely, however, that drilled shells of about 30 mm in height represent optimal prey size for naticid predators that lived in a benthic Seogwipo community.

Introduction

The surfaces of mineralized skeletons (mollusks, brachiopods, and echinoids) are often characterized by diverse borehole structures including irregular tunnels (e.g. ichnogenus *Caulostrepsis*) and circular holes (e.g. ichnogenus *Oichnus*). Some of these structures are traces produced by penetration of their surface by macroendolithic organisms for their new habitats (Polychaete and Bryozoa) or anchoring sites (Porifera), whereas others are traces produced by predatory organisms for foraging (Gastropoda). The prey–predator interactions have been extensively studied in the modern benthic realm (e.g. Schimmel et al 2012) and even in the fossil record for which direct observations are unavailable (Bromley 1981; Ceranka and Złotnik 2003; Kitchell et al 1981; Kowalewski 2004; Leighton 2002). Among the most extensively studied indicators of biotic relationships, in the fossil record, are predatory drilling holes, which have provided various aspects of the past prey–predator interactions (Baumiller 1996; Kelley and Hansen 2003; Kitchell 1986; Kowalewski 2002; Kowalewski et al 1998; Ottens et al 2012; Rohr 1991; Vermeij 1987).

One of the most commonly encountered fossil predatory traces is a millimeter-sized circular to subcircular structure on the surface of bivalve shells that is known to be a drill hole by predatory gastropods (Bromley 1981, 1993; Nielsen and Nielsen 2001; Zonneveld and Gingras 2014). The fossil record has dramatically radiated from the beginning of the Cretaceous period (Kowalewski et al 1998; Taylor and Wilson 2003), and various studies have focused on identification of predation, relationships of borehole and predator sizes, selectivity of borehole sites, and taxonomy. In this paper, we report the first record of drill holes produced by predatory gastropods on the surface of bivalve shells from the Cenozoic Seogwipo Formation, Korea. We also discuss the taxonomy of ichnospecies and other aspects of prey and predator interactions.

Geologic settings

The Seogwipo Formation is the late Cenozoic sedimentary sequence located along the southwestern coast of Seogwipo, Jejudo, Korea (Figure 1). The formation is mainly composed of pyroclastic coarse sediments including gravel sandstone and sandstone, and

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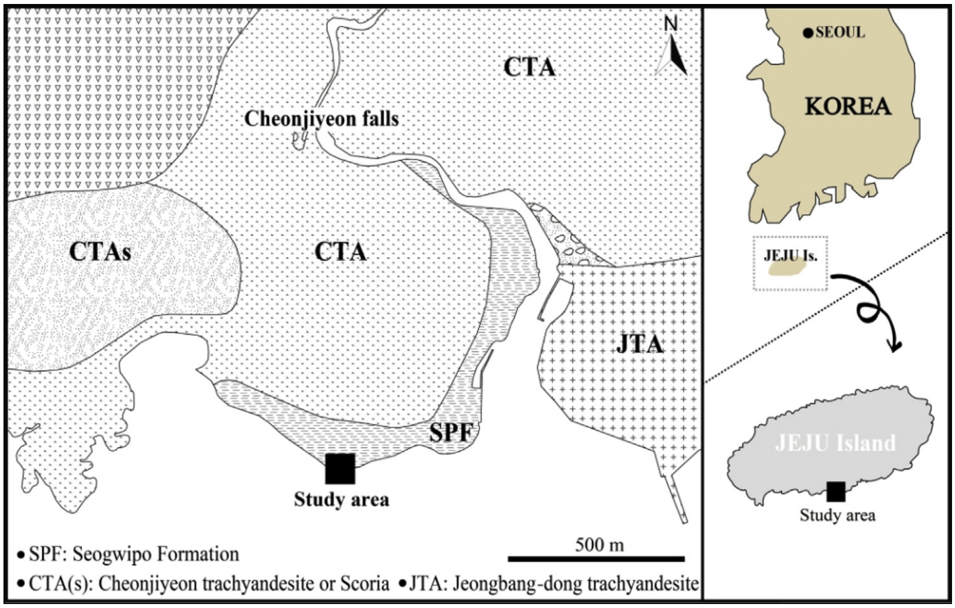

Figure 1. Locality map of Natural Monument No. 195 (shell fossil site of the Seogwipo Formation), and fossil site (black square) of the Seogwipo Formation. Is. = island.

silty mudstones are often intercalated in between the coarse sediments (Kim and Heo 1997; Yoon and Chough 2006). Analysis of sedimentary facies (Sohn and Yoon 2010; Yoon and Chough 2006) and fossil assemblages (Kang 1995) suggested that the formation had been deposited in a shallow marine (foreshore to offshore) environment. Age of the formation was obtained from paleomagnetic (Kim and Lee 2000; Min et al 1986) and various fossil studies (Yi et al 1998; Yoon 1988). Results of these studies revealed their formation during the Early Pleistocene period (0.08–0.2 Ma).

This formation is exposed only at one locality along the rock cliff of the coast near the entrance of Cheonjiyeon falls, where diverse fossils with damaged bivalve shells were collected. The outcrops have yielded diverse fossils including microfossils [foraminifera (Kang 2003) and nannofossils (Yi et al 1998)] and macrofossils [mollusks (Yoon 1988) and trace fossils (Kim and Heo 1997)]. In particular, this formation is famous for containing well-preserved and abundant bivalve shells. The Korean government designated this area as a natural monument 195 “Shell fossil site of Seogwipo Formation” in 1968.

Materials and methods

Various mineralized skeletons (bivalves, gastropods, scaphopods, brachiopods, and echinoids) occur as aggregated assemblages within some coarse sandy layers, forming fossiliferous beds throughout the Seogwipo section (Figure 2). More than 10 fossiliferous beds are recognized along the about 30-m thick and 100-m wide Seogwipo outcrop. The fossiliferous beds are mainly composed of two dominant bivalve shells: large scallops (e.g. *Mizuhopecten tokyoensis hokurikuensis*) and small white shells [e.g. *Glycymeris rotunda*; see Choi et al (1998) for further taxonomy of the shells]. Most of the circular to subcircular drill holes were detected on the surface of small white shells, especially *G. rotunda*: a few drill holes were also found on other species of small bivalves (*Megacardita coreensis* and *Acila insignis*; Figure 3). More than 50 shell specimens with drill holes were collected from the rock masses detached from the fossiliferous beds.

Pictures of drilled shells were taken under a dissecting microscope; additionally, scanning electron microscope (SEM) images were also obtained for analysis of detailed structures of drill holes. The shell length (maximum distance from the anterior margin to the posterior margin) and width (maximum distance from left to right margins) were measured using a digital caliper. To elucidate the relationships between borehole size and prey size, both outer and inner borehole diameters (OBD and IBD, respectively) were measured using a dissecting microscope with a calibrated ocular micrometer and/or scaled SEM pictures. OBD and IBD are defined as the longest distance between borehole edges across the center of the borehole.

Results

Description of drill holes

Circular to subcircular drill holes penetrating completely throughout the shells are found exclusively on the small bivalve shells (Figures 2D and 3). They are characterized by a beveled sharp edge and elliptic paraboloid in cross section (Figure 4). The OBD [4.21 mm (1.92–5.76)] is, therefore, always larger than the IBD [2.94 mm (1.5–4.34)] with a depth-to-diameter ratio less than 1 (Figure 5). The outline of both OBD and IBD edges is generally sharp with an irregular scratching. Most of the elliptic paraboloid forms are developed symmetrically to the borehole center, but deformed paraboloids with a more gentle angle on one side (anterior side of the right valve) are also observed in some specimens (Figures 3K and 4C).

Walls of some boreholes are smooth without any structures (Figures 4A and 4D), whereas those of other boreholes show etched relief-like structures (Figures 4B and 4E). In some specimens, walls decorated with microscopic pits ($\leq$30 μm) are also observed, which are probably traces of microendolithic organisms (Figure 4F). An incomplete borehole (only 1 specimen was found; Figures 3L and 4C) is characterized by a slightly raised central boss. No characteristic features are recognized on the base of incomplete borehole where a central boss is located (Figure 4C). The granular appearance observed near the central boss is likely caused by a diagenetic effect.

All boreholes occur solitarily on the shell surfaces (Figure 3). The borehole sites on the shell seem to be random in position, but more

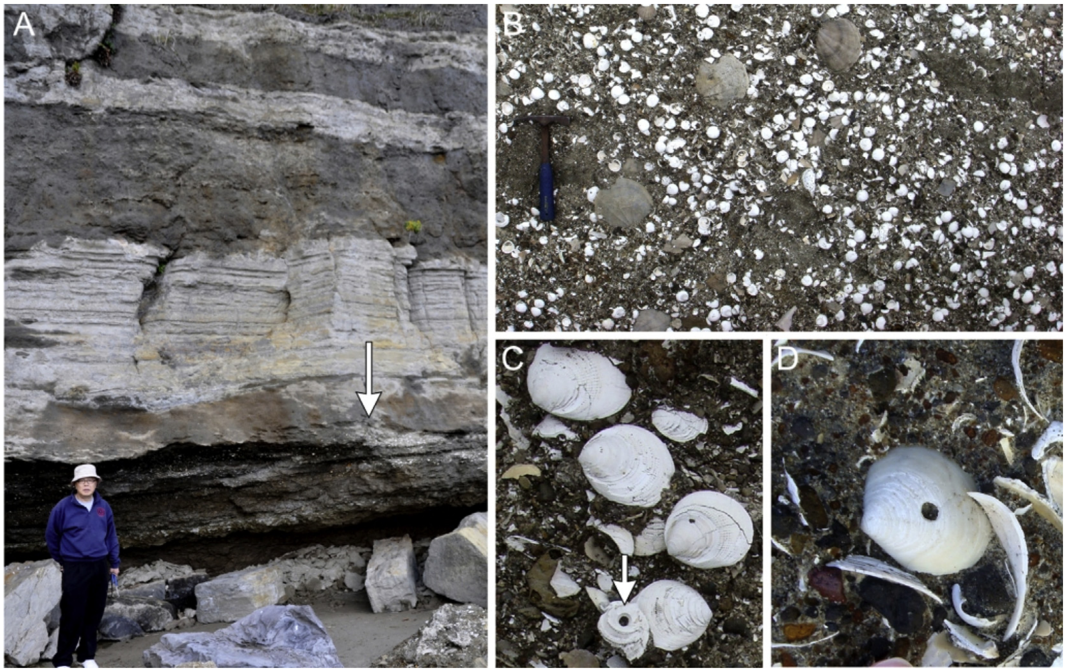

Figure 2. Outcrop of the Seogwipo Formation: A, Fossiliferous bed (white arrow) of the Seogwipo Formation; B, a dense assemblage of bivalve shells; C and D, Predatory drill holes (found on the surfaces of a bivalve shell, *Glycymeris rotunda*).

holes are positioned in the central area below an umbo than those in the marginal area (Figure 5). The positive relationships between specific drilling sites and predator size (Figure 5), and between OBD and shell height (Figure 6) are not recognized.

Systematic ichnology

All the drilled specimens were collected from one locality of the Seogwipo outcrop located near the entrance of "Cheonjiyeon falls,"

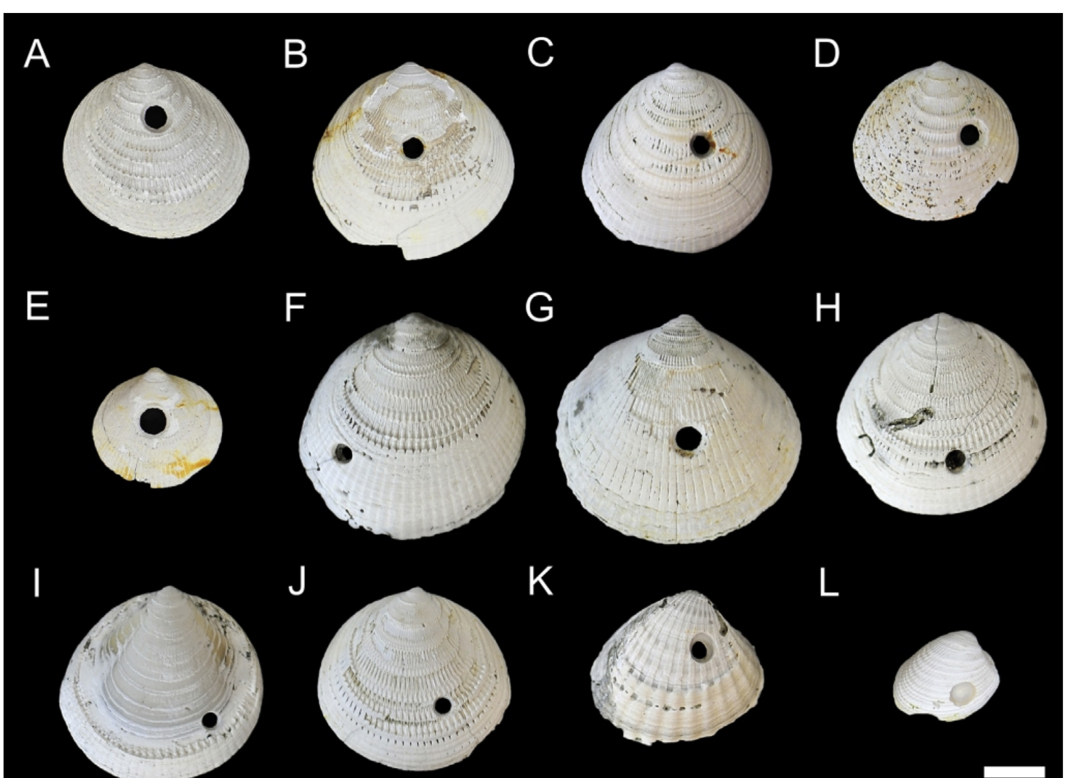

Figure 3. *Oichnus paraboloides* Bromley, 1981 collected from the Seogwipo Formation: A–J, *Glycymeris rotunda*; K, *Megacardita coreensis*; L, incomplete drill hole on *Acila insignis*. (A, NHCG 10908; B, NHCG 10909; C, NHCG 10910; D, NHCG 10911; E, NHCG 10912; F, NHCG 10913; G, NHCG 10914; H, NHCG 10915; I, NHCG 10916; J, NHCG 10917; K, NHCG 10918; L, NHCG 10919). <scale bar: 1 mm>

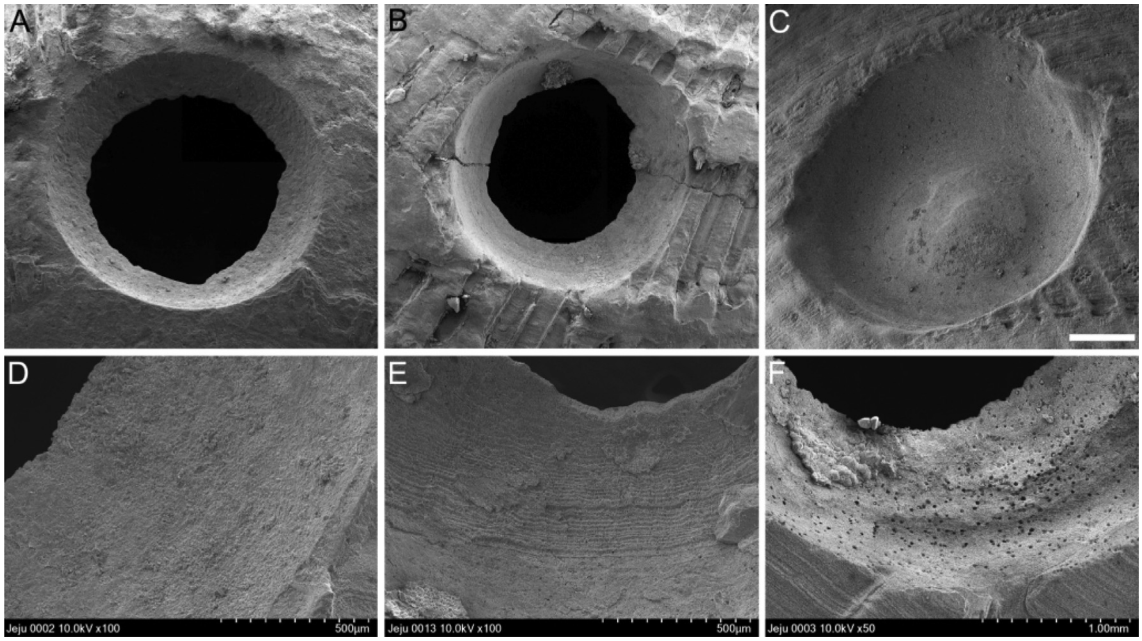

Figure 4. Scanning electron microscope pictures of *Oichnus paraboloides* showing detailed internal structures. Boreholes characterized by symmetric paraboloid (A, NHCG 10916; B, NHCG 10910) and asymmetric paraboloid (C, NHCG 10919). Three different wall types are observed: smooth wall (D, close view of A), wall with etched patterns (E, close view of B), and wall with microscopic pits (F, NHCG 10918). <scale bar in (C): 1 mm>

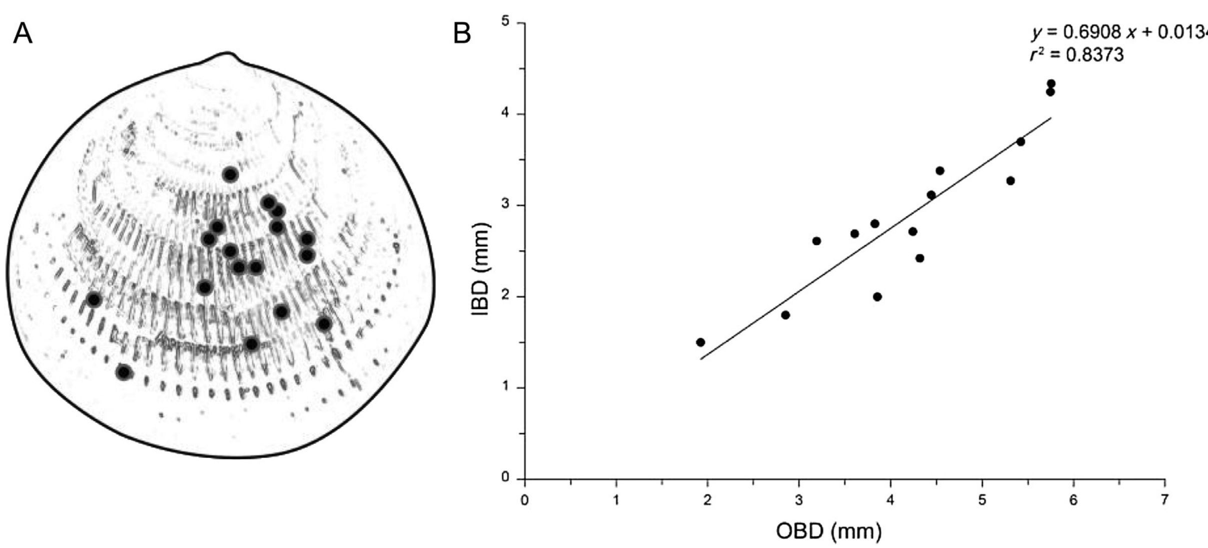

Figure 5. A, Position of *Oichnus paraboloides* on drilled shells; B, measurements of outer borehole diameter (OBD) and inner borehole diameter (IBD).

and deposited in the fossil collections of the Cultural Heritage Administration (CHA) of Korea. The selected 12 specimens presented in this paper were labeled with a collection number of CHA, prefixed by NHCG (NHCG 10908 to NHCG 10919). Taxonomy of Choi et al (1998) has been applied for prey shells. Because this is the first report concerning fossil borehole traces in Korea, we herein rewrite an emended diagnosis (Nielsen and Nielsen 2001) of an ichnogenus *Oichnus*.

Ichnogenus *Oichnus* Bromley, 1981

Type ichnospecies. *Oichnus simplex* Bromley, 1981.

Other ichnospecies. *Oichnus paraboloides* (Bromley 1981), *Oichnus ovalis* (Bromley 1993), *Oichnus halo* (Neumann and Wisshak 2009).

Diagnosis. "Circular, subcircular, oval, or rhomboidal solitary holes or pits of biogenic origin in hard substrates, commonly perpendicular to the subperpendicular to substrate surface. The holes pass directly through substrate as a penetration, whereas the pits end within the substrate as a shallow to moderately deep depression or short subcylindrical pit, commonly with a depth-to-width ratio of 1, with or without a central boss" [slightly revised by several authors after Bromley (1981), applied here Nielsen and Nielsen (2001)].

Remarks. The circular to subcircular drill hole was originally assigned to the ichnogenus *Oichnus* (Bromley 1981). Some ichnogenera for similar-looking traces were also erected, including *Sedilichnus* (Müller 1977) and *Tremichnus* (Brett 1985). Several authors (e.g. Nielsen and Nielsen 2001; Pickerill and Donovan 1998)

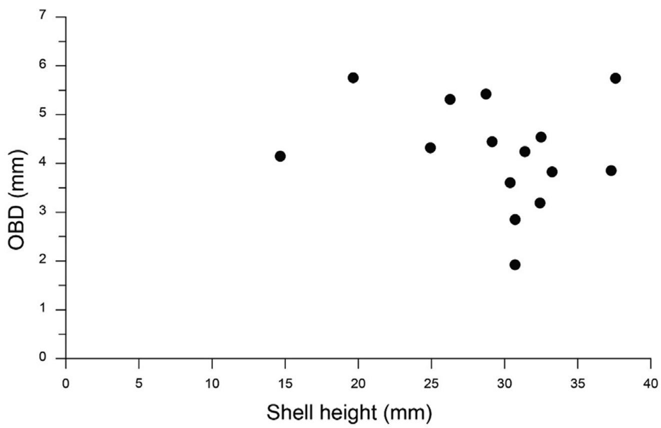

Figure 6. Relationship between shell height of prey *Glycymeris rotunda* and outer borehole diameter (OBD) of *Oichnus paraboloides*. No correlation is recognized.

suggested that *Tremichnus* should be considered as a junior synonym of *Oichnus*, and we here agree with their conclusions. Recently, Zonneveld and Gingras (2014) suggested that *Oichnus* Bromley, 1981 is a junior synonym of *Sedilichnus* Müller, 1977, and formalized a new ichnotaxonomy of *Sedilichnus*. However, most of subsequent authors (Donovan and Novak 2015; Gendy et al 2015; Klompmaker et al 2014; Rojas et al 2014; Sebastian et al 2015) still used *Oichnus* rather than *Sedilichnus*. We, in this paper, also prefer to use *Oichnus* due to its extensive usage in the literature.

Ichnospecies ***Oichnus paraboloides* Bromley, 1981**
(Figures 3A–L and 4A–F)
Oichnus paraboloides isp. nov., Bromley, 1981: 62.
Tremichnus paraboloides n. ichnospecies: Brett, 1985: 625, 627–628.
Oichnus paraboloides: Feige and Fürsich, 1991: 129.
Oichnus paraboloides: Pek and Mikulás, 1996: 109, 111.
Oichnus paraboloides: Dietl and Kelley, 2006: 104.
Sedilichnus paraboloides: Zonneveld and Gingras, 2014: 897, 900.

Materials. Of the more than 50 shell specimens with drill holes, fossil collection numbers of CHA of Korea were given to the selected 12 specimens (NHCG 10908 to NHCG 10919).
Age and locality. Early Pleistocene (0.08–0.2 Ma) in age, rock cliff exposed along the southwestern coast of Seogwipo, the Seogwipo Formation.

Diagnosis. "*Oichnus* having a spherical paraboloid form, truncated in those cases where the boring penetrates right through the substrate. Where it does not so penetrate, the paraboloid may be deformed by a slightly raised central boss" (after Bromley 1981, p 62).

Description. Outline of boreholes circular to subcircular with OBD of 4.21 mm (1.92–5.76) and IBD of 2.94 mm (1.5–4.34; Figure 5). The holes are characterized by a beveled and elliptic paraboloid in cross section with a depth-to-diameter ratio less than 1. Most are symmetrical paraboloid forms, whereas asymmetric paraboloids (Figures 3L and 4C) are rarely found. Walls smooth (Figure 4A and 4D), etched relief-like structures (Figures 4B and 4E), or sometimes decorated with microscopic pits (≤30 μm; Figure 4F). A slightly raised central boss is developed in an incomplete specimen with no characteristic features on its base (Figure 4C).

Remarks. Two different types of wall structures of this ichnospecies are also observed in Korean specimens: smooth wall (Figures 4A and 4D) and wall with etched relief-like structures (Figures 4B and 4E). As several authors mentioned (e.g. Bromley 1981), the etching patterns seem to reflect the ultrastructure of the prey shells. However, an observation that specimens of the same prey species (e.g. *G. rotunda*) often show different wall structures may suggest that different wall structures are due to different mode of penetration by different predators. At this moment, however, it is premature to separate the two different forms into two ichnospecies until more specimens showing a positive correlation of such relationships are collected.

Discussion

Predator identity

The past prey–predator interactions have often been recognized from the fossil records, particularly from the traces left on preys (Kelley and Hansen 1993; Klompmaker 2012; Klompmaker et al 2013; Kowalewski et al 1998; Morris and Bengtson 1994). It is, however, very difficult or even impossible to identify the exact predators from the traces because of (1) the unavailability of direct observations and (2) morphological simplicity and similarity of traces produced by different predators. Indeed, many of the circular to subcircular traces similar (or sometimes even identical) to *Oichnus* have been reported from the surfaces of bivalve fossils. Such traces could have been caused by different predators such as predatory gastropods (e.g. *Oichnus*), boring clionid sponges (e.g. *Entobia*), or Polychaete worms (e.g. *Caulostrepsis*).

Based on observations in modern marine environments (e.g. Ansell and Morton 1987) and laboratory experiments (e.g. Dietl and Kelley 2006; Kowalewski 2004), it has been documented that the ichnospecies *O. paraboloides* is a trace left by predatory gastropods. In particular, naticid gastropods are known to produce typical traces of *O. paraboloides* (Kowalewski 1993; Reyment 1999), although some exceptions were also reported (Dietl and Kelley 2006; Kelley and Hansen 2003). Naticids are, indeed, important predators of bivalves in a benthic infaunal community, leaving their traces on bivalve shells in the fossil record (Kelley and Hansen 1993; Kitchell 1986).

Size and gross morphology (typical parabolic cross section, Figures 3 and 4) of our specimens are almost identical to those produced by modern naticid gastropods. Another diagnostic feature of *O. paraboloides*, a central boss, is also observed in an incomplete specimen (Figures 3L and 4C). The incomplete hole indicates a failure of drilling attempt by naticid gastropods (Chattopadhyay and Dutta 2013; Kowalewski 2002). Co-occurrence of the drilled shells and some species of naticid gastropods (e.g. *Cryptonatica janthostomoides*) in the same fossiliferous horizon of the Seogwipo Formation also supports the fact that Korean *O. paraboloides* is a drilling trace produced by predatory naticid gastropods using the accessory boring organ and radula (Carriker and Gruber 1999; Guerrero and Reyment 1988).

Prey selectivity

O. paraboloides collected from the Seogwipo Formation is predominantly found on one bivalve species, *G. rotunda*, although more than 10 bivalve species with size similar to *G. rotunda* have been reported from the same locality of the Seogwipo Formation (Choi et al 1998). More than 70% of *O. paraboloides* were found on the prey shell of *G. rotunda*, and a very few traces were observed on bivalve shells bigger than the *G. rotunda*. This may explain a specific prey preference of predatory naticid gastropods, which has been repeatedly documented from the recent (Dietl and Alexander 1995; Kelley and Hansen 1996) and the fossil record (Croll 1983; Dietl and Alexander 1995; Kelley 1991).

The size of drill hole, particularly OBD, is known to be correlated with the size of individual predators of naticid (Kitchell et al 1981). This is mainly based on an assumption that the size of a drill hole reflects directly the size of an accessory boring organ of predatory gastropods (Carriker and Van Zandt 1972), and that larger predators tend to feed on larger preys (Carriker and Gruber 1999). In the case of naticid gastropods, many authors have demonstrated a correlation between size of naticid predator and OBD (Griffiths 1981; Kitchell et al 1981; Peitso et al 1994). However, analysis of shell height and OBD in this study is not consistent with results obtained in the previous laboratory experiments, showing no relationships between OBD and shell height (Figure 6). As Kowalewski (2004) mentioned, results from the laboratory experiments may not be applicable in our cases where multiple predators co-existed in a marine benthic community. However, if we consider the fact that naticid gastropods tend to select their prey to maximize energy gain (Kelley 1988; Kitchell et al 1981), it is likely that drilled shells of about 30 mm in height represent optimal prey size for the naticid predator that lived in a benthic Seogwipo community.

Most *O. paraboloides* boreholes are observed on the central area below the umbo of the prey; a few boreholes lie marginally (Figure 5). This may also reflect a borehole-site selectivity that is a quite common phenomenon in many naticid species (Cintra-Buenrostro 2012; Dietl and Alexander 1995; Kelley 1991). A high proportion of drill holes in a central area may be associated with easiness of predators handling (Ziegelmeier 1954) and/or the position of prey's adductor muscles (Chattopadhyay and Dutta 2013). However, such a selectivity is not likely to be influenced by the size of predators because no correlation between shell height and position of boreholes was observed in our fossils (Figures 5 and 6).

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